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Immature stages of high arctic *Gynaephora* species (Lymantriidae) and notes on their biology at Alexandra Fiord, Ellesmere Island, Canada

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Abstract. Two species of *Gynaephora* are found in North America and their geographic ranges overlap broadly in the Canadian Arctic. Despite numerous studies that have addressed aspects of the biology, ecology, and physiology of these species, confusion regarding identification of their immature stages, originating with the original description of the first of the two species discovered, persists even in recent literature. In this paper, for the first time, all immature stages of both species are described and most are illustrated, with emphasis on the differences between the two species that allow for their identification.

Eggs and pupae of the two species are very similar morphologically but usually may be distinguished by association with cocoons and also by size at Alexandra Fiord, Ellesmere Island. In first instar larvae, the cuticle is black in *G. groenlandica* but pale in *G. rossii*; older larvae are readily identified by distinct differences in the color patterns of the larval hairtufts and by the form of the hairs, being spinulose in *G. groenlandica* and predominantly plumose in *G. rossii*. Cocoons usually may be distinguished by color but this feature is variable while the structure of the cocoons, double-layered in *G. groenlandica* and single-layered in *G. rossii*, is definitive.

Field studies conducted at Alexandra Fiord revealed some gaps and inaccuracies in previously published life history information. Egg masses laid on cocoons were found to suffer extensive predation by birds, a source of mortality that was previously overlooked. There appear to be six larval instars in *G. rossii* but seven in *G. groenlandica* rather than six as previously reported. Seasonal activity patterns of larvae were found to differ, with *G. groenlandica* active only in the early part of the growing season and *G. rossii* remaining active in late summer. Foodplant preferences also differed, partly as a result of the different food sources available at different times during the spring and summer. Finally, larval hairs of these species have been found to have urticating properties, causing skin irritation after extensive handling of larvae or cocoons.

Key Words. *Gynaephora groenlandica*, *Gynaephora rossii*, eggs, larvae, pupae, cocoons, morphology, seasonal activity, foodplants

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Introduction

The genus *Gynaephora* Hübner (Lymantriidae) is represented in North America by two species, *G. groenlandica* (Wocke [in Homeyer] 1874) and *G. rossii* (Curtis 1835). The geographic distribution of *G. groenlandica* is almost entirely limited to Greenland and islands of the Canadian arctic archipelago; that of *G. rossii* includes most of the North American Arctic (excluding Greenland) and Siberia, with isolated populations occurring in alpine areas of Japan, New England, and the southern Rocky Mountains (Ferguson 1978, Mølgaard & Morewood 1996). *Gynaephora groenlandica* has the distinction of ranging to the most northerly point of land in Canada (Ward Hunt Island, 83°N; Downes 1964) as well as northernmost Greenland (Wolff 1964) and is considered to be a high arctic endemic species (Munroe 1956, Downes 1964) whereas *G. rossii* has a typical arctic/alpine distribution.

Early accounts of arctic *Gynaephora* species are numerous, mostly consisting of descriptions and natural history observations (Curtis 1835, Homeyer 1874, Grote 1876, Packard 1877, Scudder et al. 1879, Skinner & Mengel 1892, Dyar 1896, 1897, Nielsen 1907, 1910, Johansen 1910, Gibson 1920, Forbes 1948, Bruggemann 1958). Later authors emphasized the apparent adaptations of these insects and others to the extreme conditions of the arctic environment (Downes 1962, 1964, 1965, Oliver et al. 1964, Oliver 1968). More recent studies have investigated the biology, ecology, and physiology of arctic *Gynaephora* species in order to elucidate and understand the various ways in which they are adapted to arctic conditions (Ryan 1977, Ryan & Hergert 1977, Schaefer & Castrovillo 1979, Kevan et al. 1982, Kukal 1984, Kukal & Kevan 1987, Kukal, Heinrich & Duman 1988, Kukal, Serianni & Duman 1988, Kukal & Dawson 1989, Kukal et al. 1989, Kevan & Kukal 1993, Kukal 1995, Lyon & Cartar 1996).

Despite the attention that arctic *Gynaephora* species have received, there remains confusion regarding identification of the immature stages. For example, Kevan et al. (1982) ostensibly studied *G. rossii* but published photographs of a larva, cocoons, and even an adult that are clearly *G. groenlandica*. Furthermore, Ryan and Hergert (1977) considered the two species to be "identical in their food choices and development, and almost identical morphologically"; however, there are considerable differences, both morphologically and ecologically. The purpose of this paper is to describe and illustrate the immature stages of *G. groenlandica* and *G. rossii*, with emphasis on differences between the species, and to update information on their natural history as observed at Alexandra Fiord, Ellesmere Island, Canada.

Methods and Materials

Fieldwork was conducted at Alexandra Fiord (78° 53′ N, 75° 55′ W) on the east coast of Ellesmere Island from 6.VI.1994 to 15.VIII.1994, from 29.V.1995 to 17.VIII.1995, and from 25.V.1996 to 13.VIII.1996. The study site consists of a small (about 8 km^2) lowland valley bounded by glaciers to the south, upland polar desert and fellfield to the east and west, and the fiord itself to the north. This site has been subject to a considerable amount of ecological research (cf. Svoboda & Freed-

man 1994) and is described as a "polar oasis," noted for its relatively lush vegetation compared to the surrounding polar desert (Freedman et al. 1994). Populations of both species of *Gynaephora* occur at Alexandra Fiord, although *G. groenlandica* is far more abundant there than is *G. rossii.*

Larvae, cocoons, adults, and eggs of both species of *Gynaephora* were observed and photographed in the field and were collected for rearing and for more detailed examination. Dimensions of eggs and maximum widths of larval head capsules viewed from the front were measured to the nearest 0.05 mm using a stereomicroscope equipped with an ocular micrometer, at a magnification of 20×. Early larval instars were determined by rearing larvae from eggs and measuring head capsules shed at each moult. Head capsule width (HCW) for the final instar was determined by measuring head capsules from larvae that had been killed by parasitoids after spinning cocoons, indicating that they were in their final stadium. Mean HCW for each of the intermediate instars was estimated by extrapolating from the mean HCW of the early and final instars according to the Brooks-Dyar Rule (Dyar 1890, Daly 1985) and these estimates corresponded well with peaks in the distribution of measured HCW for *G. groenlandica.* The distribution of HCW overlapped for these intermediate instars and therefore sample statistics were calculated by dividing the HCW distribution at the low points between peaks. Due to this overlap in HCW between intermediate instars and the very limited number of actual HCW measurements for the intermediate instars of *G. rossii,* the given HCW for these instars should be considered approximations only. Descriptions of the later instars were obtained by measuring the head capsules of larvae examined in detail and assigning these larvae to the appropriate instar. These descriptions were supplemented with field observations of larval phenotypes, especially larvae that were spinning cocoons, indicating that they were in their final stadium. Descriptions of larvae follow the terminology used by Ferguson (1978).

Photographs of larval hairs and portions of cocoons were taken through a stereomicroscope at a magnification of 30×. Maximum lengths and widths of cocoons viewed from above were measured to the nearest millimeter using a plastic ruler; sexes were subsequently determined from the morphology of caudal segments of the pupal exuviae (cf. Fig. 1). Maximum lengths and widths of pupae in ventral view were measured to the nearest half millimeter using a plastic ruler; very few pupae were measured because most were left to develop within their cocoons for other studies. Descriptions of pupae follow the terminology of Mosher (1916) and were formulated to be comparable to those published by Patočka (1991). Measurements are given as mean ± standard deviation, followed by the sample size in brackets, and are rounded off to the level of precision of the original measurements; statistical tests were conducted as described by Zar (1984) before rounding off the data.

Foodplant preferences were determined by recording the plant species and part of the plant eaten by all *Gynaephora* larvae that were observed actively feeding on the tundra in 1995 and 1996; these observations were limited to free-ranging larvae.

Results

Descriptions of Immature Stages

Eggs. Eggs laid in masses covered by hairs rubbed from the abdomen of

the female, typically on the cocoon from which the female emerged but also frequently on vegetation or the ground (Plate 1). Eggs of both species smooth, creamy white, and roughly spherical but somewhat flattened.

***G. groenlandica*:** 1.60 ± 0.05 mm in diameter by 1.35 ± 0.05 mm in height (n = 10).

***G. rossii*:** 1.40 ± 0.05 mm in diameter by 1.10 ± 0.05 mm in height (n = 10).

Eggs of *G. rossii* significantly smaller than those of *G. groenlandica* ($t_{(1)18}$ = 15.345, $P < 0.0005$ for diameter; $t_{(1)18}$ = 15.545, $P < 0.0005$ for height), this difference visible even to the unaided eye.

Larvae. Larvae of both species large and very hairy, superficially resembling larval Arctiidae (Plate 2). The following general description, outlining the basic arrangement of verrucae and hairs, applicable to all instars of both species; modifications and species-specific differences described in the subsequent sections. Differences only noted in the specific descriptions; larvae of a given instar correspond to the description given for the previous instar except as described otherwise.

Head capsule black and bearing many hairs. Addorsal, subdorsal, supraspiracular, subspiracular, and subventral verrucae present on mesothorax, metathorax, and abdominal segments 1 through 8. Addorsal verrucae fused with subdorsal verrucae on prothorax and abdominal segment 9. On prothorax, supraspiracular verrucae greatly reduced, sometimes lacking hairs, and subspiracular verrucae enlarged and oriented anteriorly. Except as just noted, all verrucae bearing from one to many hairs. Hairs arising from addorsal and subdorsal verrucae generally thicker than those arising from supraspiracular, subspiracular, and subventral verrucae. Hairs arising from supraspiracular and subspiracular verrucae, and from dorsal verrucae on abdominal segment 9, up to two or three times as long as the longest hairs arising from addorsal, subdorsal and subventral verrucae. Cuticle, including verrucae, entirely black except where noted below. Dorsal glands on abdominal segments 6 and 7 whitish and well developed in all instars except the first.

***G. groenlandica*:** First instar HCW = 0.70 ± 0.05 mm (n = 140). Corresponding to the general description above. Cuticle between verrucae black. Hairs arising from addorsal and subdorsal verrucae black, hairs arising from subspiracular and subventral verrucae brown, and hairs arising from supraspiracular verrucae mixed. All hairs spinulose.

Second instar HCW = 0.95 ± 0.05 mm (n = 85). All verrucae bearing a mixture of black and brownish yellow hairs. Hairs arising from supra-spiracular, subspiracular, and subventral verrucae predominantly yellow. Hairs arising from addorsal and subdorsal verrucae predominantly yellow on mesothorax and metathorax, black on abdominal segments 1, 2, and 8, and yellow on abdominal segments 3 through 5.

Third instar HCW = 1.30 ± 0.05 mm (n = 30). Hairs more dense than in previous instars, beginning to obscure underlying verrucae from which they

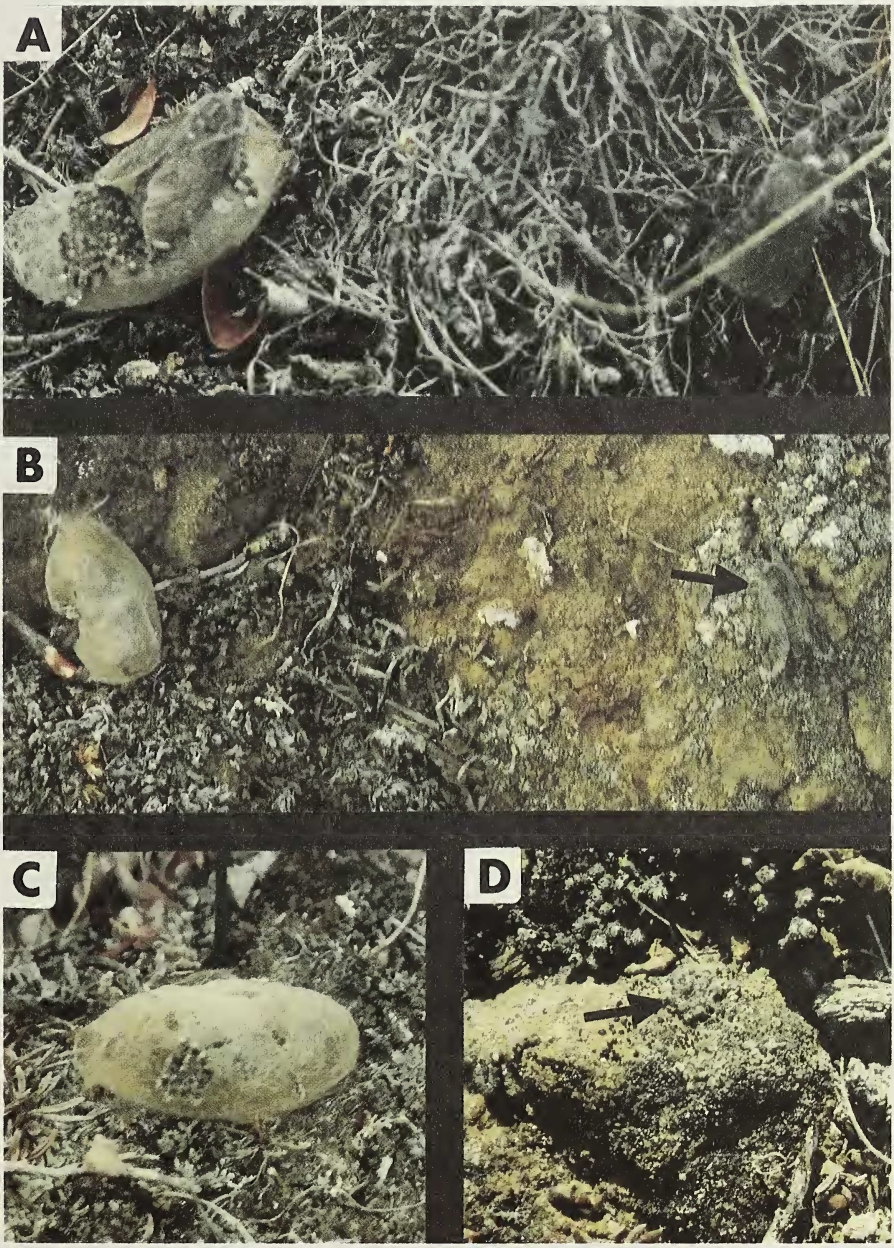

Plate 1. *Gynaephora groenlandica* (A–D). Female ovipositing on the cocoon from which she emerged; male still present to the right (A). Female (arrow) ovipositing on the ground near the cocoon from which she emerged (B). Egg mass partially depredated by foraging birds; note small tears in the cocoon where eggs were removed (C). Egg mass (arrow) on a lichen-covered rock (D).

arise. Predominance of black and yellow hairs in separate tufts, as noted in the second instar, more pronounced.

Fourth instar HCW = 1.85 ± 0.10 mm (n = 46). All hairs brown except the following. Black hairs arising from mesal portions of addorsal and subdorsal verrucae on abdominal segments 1, 2, and 8 forming tufts much denser and somewhat longer than surrounding dorsal hairs. Yellow hairs arising from addorsal verrucae on abdominal segments 3 and 4 forming tufts denser but not longer than surrounding dorsal hairs.

Fifth instar HCW = 2.35 ± 0.15 mm (n = 230); sixth instar HCW = 3.10 ± 0.20 mm (n = 353). Hairs longer and denser than fourth instar, most notably hairs arising from supraspiracular, subspiracular, and subventral verrucae, and dorsal verrucae on abdominal segment 9. Some hairs arising from dorsal verrucae on prothorax and from subdorsal verrucae on mesothorax and metathorax as long as hairs arising from supraspiracular verrucae. Lengths of black and yellow dorsal tufts somewhat variable, sometimes nearly even and sometimes with black tufts distinctly longer than yellow. Black tuft on abdominal segment 8 longer and more slender than those on abdominal segments 1 and 2, resembling more the rudimentary hair pencil that it represents (Plate 2A).

Seventh instar HCW = 3.95 ± 0.20 mm (n = 235). Color pattern of dorsal hairtufts on abdominal segments 1 through 5 somewhat variable. Typically, on abdominal segments 1 through 4, hairs arising from addorsal verrucae black and those arising from subdorsal verrucae black mesally and yellow laterally; occasionally this pattern developed to a lesser extent also on abdominal segment 5. This produces an overall appearance of four, or occasionally five, central black tufts fringed laterally with yellow (Plate 2B). Rarely, the pattern of two black tufts on abdominal segments 1 and 2, followed by two yellow tufts on abdominal segments 3 and 4, retained in this final instar.

With the exception of the distinctive black and yellow tufts, the larval hairs of *G. groenlandica* show considerable variation in overall color, depending on how recently an individual has moulted. Freshly moulted larvae appear silvery brown overall but the brown hairs quickly darken and then very gradually fade to golden yellow (Plate 2C) during the course of the stadium.

***G. rossii*:** First instar HCW = 0.60 ± 0.05 mm (n = 44). Corresponding to the general description above. Cuticle between verrucae pale. Hairs uniformly grey in color. All hairs spinulose.

Second instar HCW = 0.85 ± 0.05 mm (n = 41). Some hairs arising from addorsal verrucae on abdominal segments 1, 2, and 8 plumose. One or two hairs arising from supraspiracular verrucae on each abdominal segment plumose. All other hairs spinulose. Cuticle generally somewhat paler between verrucae.

Third instar HCW = 1.25 ± 0.05 mm (n = 26). Hairs more dense than in previous instars, beginning to obscure underlying verrucae from which they arise. Some hairs arising from addorsal verrucae on mesothorax and metathorax, as well as abdominal segments 1, 2, and 8, plumose. Some hairs

arising from subdorsal verrucae and most hairs arising from supraspiracular and subspiracular verrucae on all segments except prothorax plumose. Other hairs spinulose, either black or yellow, those arising from thoracic verrucae and from addorsal verrucae on abdominal segments 3 through 5 predominantly yellow.

Fourth instar HCW approximately 1.75 mm. Grey plumose hairs denser and more prominent, otherwise very similar to third instar.

Fifth instar HCW approximately 2.50 mm. Some to most hairs arising from all verrucae plumose. Hairs arising from addorsal and subdorsal verrucae quite uniform in length, giving a "clipped" appearance in lateral view. Hairs arising from supraspiracular and subspiracular verrucae up to twice as long as those arising from dorsal verrucae. Longer plumose hairs grey, shorter spinulose hairs black or yellow, as in the third and fourth instars.

Sixth instar HCW = 3.55 ± 0.20 mm (n = 202). All hairs black except as noted in the following. Thoracic verrucae bearing a mixture of black and yellow hairs not forming distinct tufts. Addorsal and subdorsal verrucae on abdominal segments 1 through 8 bearing dense tufts of relatively short hairs, those arising from addorsal verrucae and the mesal portion of subdorsal verrucae black, and those arising from the lateral portion of the subdorsal verrucae yellow. This produces the appearance of a black tuft fringed laterally with yellow on each abdominal segment, the pattern becoming less distinct caudally. Variable numbers of longer grey plumose hairs arising from all verrucae, usually obscuring the pattern of black and yellow tufts to some extent, sometimes completely, and giving the impression of lint accumulated among the larval hairs (Plate 2D). In rare individuals, grey plumose hairs replaced by black spinulose hairs which do not obscure the pattern of black and yellow tufts (Plate 2E). Rearing of such larvae produced either adults of *G. rossii* or adults of the tachinid parasitoid *Chetogena gelida* (Coquillett), which is extremely host-specific to larvae of *G. rossii*, at least at this site (Morewood, unpub. data).

In general, larvae of *G. rossii* smaller than larvae of *G. groenlandica* and with much shorter hairs of more uniform length. Pattern of black and yellow dorsal hairtufts quite different in the two species and not obscured by other hairs in *G. groenlandica* but usually obscured at least partially by grey plumose hairs in *G. rossii*. Long spinulose (Plate 3A) or plumose (Plate 3B) larval hairs characteristic of *G. groenlandica* and *G. rossii*, respectively, producing a contrast in overall appearance and also quite distinct when viewed under magnification. These hairs also readily distinguished after they have been incorporated into cocoons (Plate 3C&D).

Cocoons. Cocoons spun on the surface of the tundra and anchored to the substrate, not concealed in any way but rather located in exposed sites with maximum insolation, on substrates of vegetation, litter, bare soil, or rock. Cocoons of *G. groenlandica* much larger than those of *G. rossii* (Plate 3E), mainly due to the difference in structure (see below).

***G. groenlandica*:** Cocoons constructed in two distinct layers with a consid-

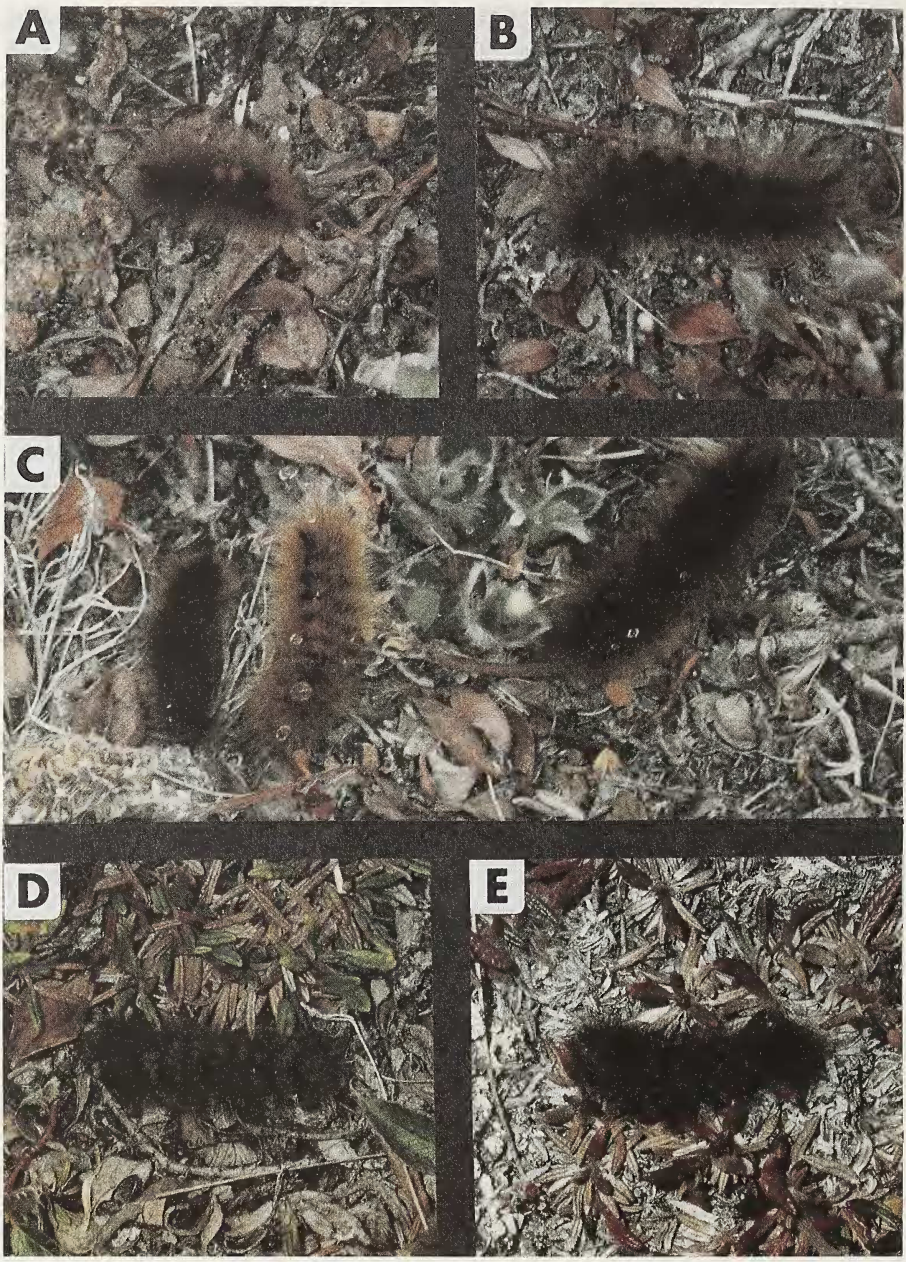

Plate 2. *Gynaephora groenlandica* (A–C) and *Gynaephora rossii* (D–E). Fifth instar larva (head to the right) with the characteristic black and yellow dorsal hairtufts and rudimentary dorsal posterior hair pencil (A). Seventh instar larva (head to the left) with the four black dorsal hairtufts typical of the final instar (B). Larvae showing the range of color of larval hairs with the most recently moulted larva on the left (C). Typical larva, showing grey tufting produced by the plumose larval hairs (D). Larva lacking grey plumose hairs (E).

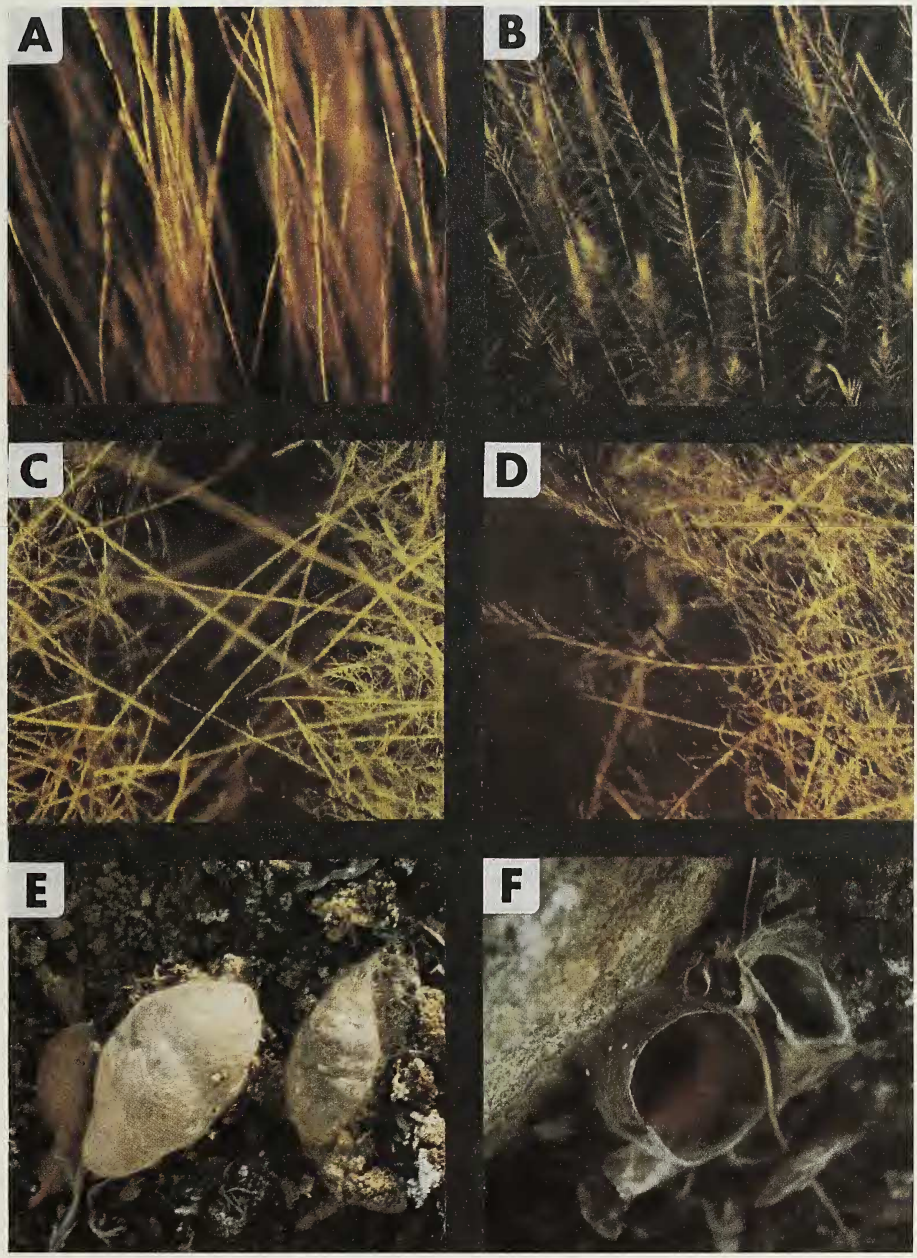

Plate 3. *Gynaephora groenlandica* (A, C, E, F) and *Gynaephora rossii* (B, D, E). Spinulose larval hairs (A). Plumose larval hairs (B). Portions of the outer (right) and inner (left) layers of the pupal cocoon (C). A portion of the pupal cocoon (D). Complete cocoons of *G. groenlandica* (left) and *G. rossii* (right) (E). Larval hibernacula; the opening in the occupied hibernaculum was the result of removing an overlying rock (F).

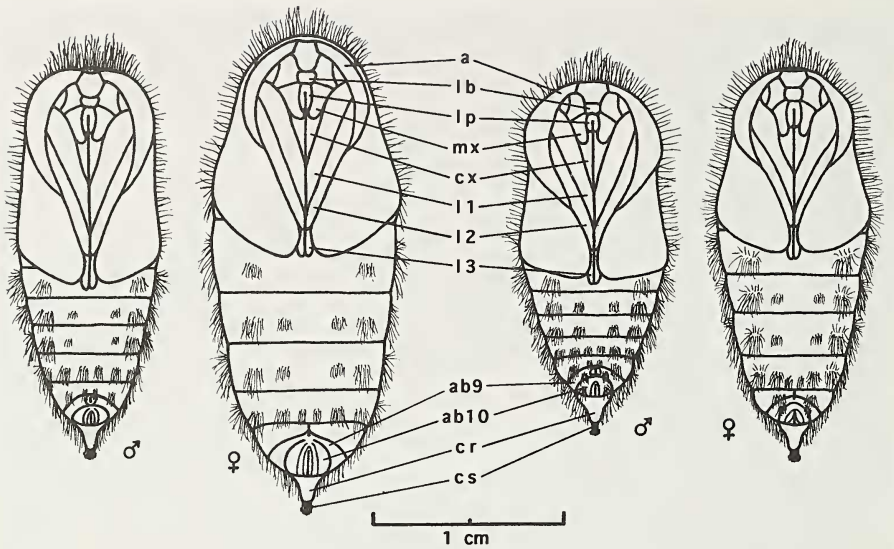

Fig. 1. Pupae of *Gynaephora groenlandica* (left) and *Gynaephora rossii* (right) in ventral view. Abbreviations: a = antenna, ab = abdominal segment, cr = cremaster, cs = cremastral setae, cx = coxa of the prothoracic leg, l1 = prothoracic leg, l2 = mesothoracic leg, l3 = metathoracic leg, lb = labrum, lp = labial palp, mx = maxilla.

erable air space between the layers. Outer layer ovoid, dimensions 32 ± 3 mm in length by 19 ± 2 mm in width (n = 279), comprised of a thin layer of silk with some larval hairs, cream colored to deep yellow or grey, depending on the number and relative proportions of black and yellow larval hairs incorporated and the extent of weathering. Inner layer oblong-ovoid, dimensions 28 ± 3 mm in length by 13 ± 1 mm in width (n = 279), comprised mainly of larval hairs tied together with silk and correspondingly deeper in color than the outer layer. Cocoons of females, with outer layer dimensions of 34 ± 3 mm by 20 ± 2 mm and inner layer dimensions of 30 ± 2 mm by 14 ± 1 mm (n = 124), significantly larger ($t_{(1)277}$ = 6.463 for outer length, 3.576 for outer width, 12.970 for inner length, 9.770 for inner width; $P < 0.0005$ in all cases) than those of males, with outer layer dimensions of 31 ± 3 mm by 19 ± 2 mm and inner layer dimensions of 26 ± 2 mm by 13 ± 1 mm (n = 155).

***G. rossii*:** Cocoons constructed in a single layer roughly equivalent to the inner cocoon of *G. groenlandica*, oblong-ovoid, dimensions 26 ± 2 mm in length by 13 ± 1 mm in width (n = 56), comprised of a single layer of silk with many larval hairs incorporated, dark grey to light grey, depending on the extent of weathering. Cocoons of females, with dimensions of 27 ± 2 mm by 13 ± 1 mm (n = 17), significantly larger ($t_{(1)54}$ = 2.852, $0.0025 < P < 0.005$ for length; $t_{(1)54}$ = 2.143, $0.01 < P < 0.025$ for width) than those of males, with dimensions of 25 ± 2 mm by 12 ± 1 mm (n = 39).

Pupae. Pupae of both species (Fig. 1) reddish-brown, darkening to black as the pharate adult matures but often retaining some areas of reddish-brown cuticle, most notably along caudal margins of abdominal segments. Very hairy; hairs arising from scars of larval verrucae, brown to golden yellow and always simple, not plumose or spinulose. Dorsal hairs long, dense, and erect; ventral hairs much shorter, sparser, and recumbent. Labrum trapezoidal with rounded corners, caudal margin varying from straight to strongly concave. Maxillae short, slightly longer than labial palps; coxae of prothoracic legs distinctly visible caudad of maxillae. Prothoracic legs (excluding coxae) border on each other for about as long as length of maxillae. Antennae short, extending only about halfway to caudal margin of wings. Wingtips separated by ends of metathoracic legs. Ventral surface of abdominal segments 9 and 10 tapering steeply towards cremaster. Cremaster short and conical, somewhat flattened dorsoventrally, apex rounded and bearing a group of short, hooked setae.

***G. groenlandica*:** Pupae with dorsal hairs up to 4 mm in length and ventral hairs up to 2 mm in length. Hairs usually absent from ventral surface of abdominal segment 9 and always absent from ventral surface of abdominal segment 10. Maxillae usually curving mesad and often meeting beyond ends of labial palps. Ventral surface of cremaster with fine longitudinal grooves in females, less apparent in males. Female pupae, with dimensions of 24.0 ± 2.0 mm in length by 9.5 ± 0.5 mm in width (n = 3), significantly larger ($t_{(1)4} = 3.255$, $0.01 < P < 0.025$ for length; $t_{(1)4} = 7.071$, $0.001 < P < 0.0025$ for width) than male pupae, with dimensions of 19.5 ± 1.0 mm in length by 7.5 ± 0.5 mm in width (n = 3).

***G. rossii*:** Pupae with dorsal hairs up to 3 mm in length and ventral hairs up to 1.5 mm in length. Hairs always present on ventral surface of abdominal segment 9 and usually present on ventral surface of abdominal segment 10. Maxillae roughly straight or slightly curved mesad but never meeting beyond ends of labial palps. Ventral surface of cremaster smooth. Female pupae, with dimensions of 19.0 ± 1.0 mm in length by 8.0 ± 0.5 mm in width (n = 2), larger than male pupae, with dimensions of 17.0 ± 1.0 mm in length by 7.0 ± 0.5 mm in width (n = 3), the difference statistically significant for length ($t_{(1)3} = 2.402$, $0.025 < P < 0.05$) but not for width ($t_{(1)3} = 2.049$, $0.05 < P < 0.10$), probably due, at least in part, to the small sample size.

Pupae of *G. groenlandica* generally larger than those of *G. rossii*, the difference being more pronounced for females ($t_{(1)3} = 3.349$, $0.01 < P < 0.025$ for length; $t_{(1)3} = 5.563$, $0.005 < P < 0.01$ for width) than for males ($t_{(1)4} = 3.545$, $0.01 < P < 0.025$ for length; $t_{(1)4} = 2.121$, $0.05 < P < 0.10$ for width). Considerable variation was seen among individuals in exact shapes and relative dimensions of morphological features, even in the small number of pupae examined in detail. Therefore, differences between species, as described above, were limited to those most consistent and clearly visible; nonetheless, these differences should be regarded with caution.

Differences between *G. groenlandica* and *G. rossii* in the immature stages are outlined in Table 1. Voucher specimens, including eggs, most larval

Table 1. Morphological differences between high arctic *Gynaephora* species in the immature stages. For measurements, the full range found in this study is given.

Stage **Morphological feature**	*G. groenlandica*	*G. rossii*
Eggs		
Diameter (mm)	1.55–1.70	1.35–1.45
Height (mm)	1.30–1.40	1.05–1.15
Larvae		
Head capsule width (mm)		
First instar	0.60–0.80	0.55–0.65
Second instar	0.90–1.05	0.75–0.90
Third instar	1.15–1.40	1.20–1.35
Fourth instar	1.50–2.00	ca. 1.75
Fifth instar	2.00–2.70	ca. 2.50
Sixth instar	2.70–3.60	2.90–4.15
Seventh instar	3.35–4.45	N/A[1]
Cuticle between verrucae		
First instar	black	pale
Second instar	black	paler than verrucae
All subsequent instars	black	black
Form of larval hairs		
First instar	all spinulose	all spinulose
Second instar	all spinulose	some plumose
All subsequent instars	all spinulose	many plumose
Color of larval hairs		
First instar	black and brown	uniformly grey
All subsequent instars	varying shades of brown with distinct dorsal tufts of black and yellow	longer plumose hairs grey, shorter hairs black and yellow
Cocoons		
Color	cream to deep yellow, occasionally grey	grey
Outer layer		
length (mm)	25–40	21–30
width (mm)	14–26	11–16
Inner layer		
length (mm)	19–35	N/A[1]
width (mm)	10–17	N/A[1]
Pupae		
Length (mm)	19.0–26.0	16.0–19.5
Width (mm)	7.5–9.5	7.0–8.0

[1]N/A = not applicable; these stages or structures do not occur in *G. rossii.*

instars, pupae, cocoons, and adults of both species, have been submitted to the Canadian National Collection of Insects, Ottawa, Ontario.

Natural History

Both species spin cocoons and pupate, adults emerge, mate, and lay eggs, and eggs hatch all within a single summer season lasting little more than two months; however, larval development is spread over a number of years with larvae overwintering in each stadium (Kukal & Kevan 1987; Morewood & Ring, submitted).

Fully grown larvae begin spinning cocoons very soon after becoming active in the spring. An exceptionally heavy snow accumulation in east-central Ellesmere Island during the winter of 1994–95, combined with a relative lack of wind, left the Alexandra Fiord lowland covered by a near-complete blanket of snow at the end of May. Judging by the extremely limited extent of snow-free ground and the subsequent rate of snowmelt, larvae found active upon our arrival 28.V.1995 could not have been active for more than a few days prior; however, some of these larvae had begun spinning cocoons as early as 29.V.1995. Cocoons may be completed within one day or may require two or three days for completion. Similarly, pupation may occur within one day of the cocoon being completed or may be delayed for two or three days. Pupal development, from pupation to adult emergence, of *G. groenlandica* required 15 ± 5 days (n = 53) in the field in 1995; only two *G. rossii* could be monitored for the complete period of pupal development and these required 10 and 16 days. The variation in time required for these developmental stages is due, at least in part, to variations in weather conditions, with cool and/or cloudy weather retarding activity and development.

Adults of both sexes have fully developed wings and males are strong fliers; however, females fly very little and when they do, scarcely get off the ground. Normally a female remains on her cocoon until she attracts a male and, once mated, will often lay a mass of eggs there (Plate 1A). Additional eggs are laid nearby on vegetation or on the ground, with no apparent discrimination among potential oviposition sites, and some females leave their cocoons even before laying their initial egg masses (Plate 1B). Of nine initial egg masses laid in the field in 1996, four were laid on cocoons whereas five were not. Eggs laid on cocoons are very conspicuous and suffer heavy predation by birds (Plate 1C), primarily snow buntings (*Plectrophenax nivalis* Linnaeus), by far the most abundant breeding birds at Alexandra Fiord (Freedman 1994). Of 39 egg masses found on cocoons during the summer of 1994, 26 showed signs of predation and a further 11 were completely removed before they could be protected with netting; only two egg masses were protected before apparently suffering any predation. In contrast, egg masses laid on the ground are quite cryptic (Plate 1D) and none of these egg masses were found to suffer any predation.

Embryonic development, as measured from the day that an initial egg mass was laid to the day that the first larvae eclosed, for *G. groenlandica* was 28 ± 5 days (n = 10) in the field in 1995; for *G. rossii* only one female was observed to lay an egg mass in the field and this required 31 days to begin hatching. Upon hatching, neonates usually eat a portion, often most but rarely all, of the chorion from which they emerged.

With the exception of neonates, larvae of *G. groenlandica* are active for only a relatively short portion of the growing season, after which they spin hibernacula and become dormant until the following spring. Regular surveys, combined with incidental observations, indicated that the bulk of the larval population was active only until the third week of June in 1994, the

fourth week of June in 1995, and the second week of July in 1996 due to a very late and prolonged snowmelt. Very few *G. groenlandica* larvae were found active on the tundra after 1.VII.94, 15.VII.95, and 19.VII.96, and none were found after 1.VIII.94, 31.VII.95, and 4.VIII.96. In contrast, larvae of *G. rossii* remain active late in the growing season, with active larvae observed regularly on the tundra until and including 15.VIII.94, 17.VIII.95, and 13.VIII.96, our last days of fieldwork each year. In all three years, with the exception of fully grown larvae that were spinning cocoons in June, more *G. rossii* larvae were found active in August than in June and July combined.

Gynaephora larvae were observed feeding on 11 different species of plants, representing seven different plant families (Table 2). For *G. groenlandica*, *Salix arctica* represented 87% of the feeding observations, most of these being buds and expanding leaves, with *Dryas integrifolia* representing 7%, *Saxifraga oppositifolia* representing 3%, and the remainder represented by single or very few observations. The few feeding observations for *G. rossii* were almost evenly split between *S. arctica* and *D. integrifolia*, with a single observation of a larva feeding on developing fruits of *Cassiope tetragona* on the tundra (Table 2).

Hibernacula of *Gynaephora* larvae are spun with silk, much like pupal cocoons except that no larval hairs are incorporated and the structure consists of a single layer in both species. Larvae that are confined within enclosures on the tundra generally spin hibernacula in clumps of vegetation or in litter and incorporate litter into the structure, making it extremely cryptic. Such hibernacula are rarely found on the open tundra, probably due to their cryptic nature; however, hibernacula are commonly found beneath or between loosely piled rocks (Plate 3F).

Larvae and cocoons of *Gynaephora* generally may be handled with impunity; however, the larval hairs can cause skin irritation. Extensive work dissecting parasitoid-killed larvae or tearing open cocoons, which contain larval hairs, resulted in small (1–2 mm diameter) itchy blisters, particularly on the sensitive skin between the fingers, and these blisters persisted for many days.

Discussion

Identification of Immature Stages

Confusion concerning identification of immature stages of North American *Gynaephora* species dates back to the original description of *G. rossii*. Curtis (1835) described an adult male in some detail and provided a color illustration that leaves no doubt that the species was *G. rossii*. In contrast, his descriptions of immature stages were rather cursory; however, the "two tufts of black hair on the back [of the caterpillar], followed by two of orange" are unmistakably those of *G. groenlandica*. His description of the cocoons is unfortunately too generalized to assign to either species. The original description of *G. groenlandica*, on the other hand, includes a mention of "the characteristic *Dasychira*-caterpillar hairtufts on the back and the *end segment*" (emphasis added) typical of the larvae of this species (Homeyer

Table 2. Plants on which *Gynaephora* larvae were observed feeding at Alexandra Fiord, Ellesmere Island, during the spring and summer of 1995 and 1996.

Plant species Part eaten	Number of observations *G. groenlandica*	 *G. rossii*
Salix arctica Pallas (Salicaceae)		
Buds (unopened)	99	0
Expanding leaves	166	1
Developing catkins	48	0
Mature leaves	6	2
Senescent leaves	0	3
Dryas integrifolia M. Vahl (Rosaceae)		
Leaves	24	5
Flower petals	1	0
Saxifraga oppositifolia Linnaeus (Saxifragaceae)		
Flowers	9	0
Leaves	3	0
Oxyria digyna (Linnaeus) Hill (Polygonaceae)		
Leaves	1	0
Arctagrostis latifolia (R. Brown) Grisebach (Gramineae)		
Leaves	1	0
Festuca brachyphylla Schultes (Gramineae)		
New shoots	1	0
Luzula confusa Lindeberg (Juncaceae)		
Leaves	2	0
Flower head	1	0
Luzula arctica Blytt (Juncaceae)		
Leaves	1	0
Flower stalk	1	0
Potentilla hyparctica Malte (Rosaceae)		
Flower	1	0
Vaccinium uliginosum Linnaeus (Ericaceae)		
Leaves	1	0
Cassiope tetragona (Linnaeus) D. Don (Ericaceae)		
Developing fruits[1]	0	1
Total number of observations	**366**	**12**

[1]Developing fruits were also accepted as food by *G. rossii* larvae held in the laboratory; foliage and mature fruits were not.

1874). Packard (1877) described all stages of what he thought was *G. rossii*, based on specimens collected in northern Greenland. These descriptions are fairly accurate for *G. groenlandica* and Packard himself noted that the adults differed from the description of *G. rossii* given by Curtis (1835) in that their hind wings had no "broad, blackish margin," which is perhaps the most obvious difference between adults of *G. groenlandica* and *G. rossii* (cf. Plate 1 in Ferguson 1978). The brief descriptions published by Scudder et al. (1879) as representing *G. rossii* are inadequate for identification of the species; however, they did note that the original "description of the larva does not well accord with the present specimen." It may be that neither Packard (1877) nor Scudder et al. (1879) knew of *G. groenlandica*, considering that the description of this species was published in 1874 in Germany and therefore may not have been available to them.

As early as 1875, *G. rossii* had been found above treeline on Mount Washington, New Hampshire, and recognized as the same species as had been described from the Arctic (Grote 1876). Later, Dyar (1896) described larvae from the same locality and noted that they differed from the descriptions published by both Curtis (1835) and Packard (1877). The following year, he received larvae from Greenland that agreed with Curtis' description, obtained an adult *G. groenlandica* from one of them, and concluded that "Curtis must have mixed the species" (Dyar 1897).

Despite Dyar's conclusion and his fairly detailed descriptions of the larvae of *G. rossii* (Dyar 1896) and *G. groenlandica* (Dyar 1897), misidentifications and confusing information may be found in much more recent published literature, as noted in the introduction to this paper. In addition, Ryan (1977) and Ryan and Hergert (1977) presented a photograph of a number of specimens from Truelove Lowland, Devon Island, that included both species of *Gynaephora*, but the adults were not shown associated with their cocoons. Both "light and dark color cocoons" were illustrated and Ryan and Hergert (1977) stated that "both forms [were] found with each species"; however, they made no mention of the structure of the cocoons and submitted only a single specimen (a *G. groenlandica* female with the cocoon from which it emerged) to the Canadian National Collection of Insects. As described above, cocoons of both species may be light or dark in color, depending on the extent to which larval hairs of different colors are incorporated into the cocoon and the extent to which the cocoons are weathered, but the structure of the cocoon is species-specific. Descriptions of larvae provided by Ferguson (1978) are accurate, even though they were based on extremely limited material; however, they may give the impression that the differences between the two species are rather subtle when in fact these differences produce a distinctive appearance for each species that is discernible even from a distance.

Pupae of *G. groenlandica* and *G. rossii* have not been described previously, but both species may be identified to genus using the key to genera provided by Patočka (1991). They also fit the generic description of *Gynaephora* pupae except that their antennae are apparently much shorter than those of the European species *Gynaephora selenitica* (Esper), as described and illustrated by Patočka (1991). The diagrams presented here (Fig. 1) are composites that attempt to illustrate "typical" pupae for both sexes of both North American species; however, a considerable amount of individual variation was seen, even among the small number of pupae examined. The only differences between species that were obvious and consistent were overall size and the length of hairs (which may be related to overall size), the presence or absence of hairs on the ventral surface of abdominal segments 9 and 10, and possibly the form (curved or relatively straight) of the maxillae.

It should be noted that the size differences between the two species may not be consistent across their entire range. In fact, the adults illustrated by Ferguson (1978) clearly show that *G. rossii* may be larger than *G. groenlandica* from different localities. The fact that *G. rossii* were found to be consistently

smaller than *G. groenlandica* in the current study may reflect the fact that this population of *G. rossii* is in the extreme northern portion of the species' range whereas Alexandra Fiord is more central in the distribution of *G. groenlandica.*

Despite the confusion that is apparent in the literature, most of the immature stages of arctic *Gynaephora* species can be identified to species quite readily and with little more than a cursory examination. The occasional lack of grey plumose hairs in *G. rossii* larvae may cause some confusion and may be responsible for a report of "morphs intermediate between the two ... species" (Kukal 1994), although the supposed intermediate morphs were not described in that report. The species may be reliably separated by differences in the patterns of black and yellow hairtufts and the much longer overall hairs of *G. groenlandica.* Furthermore, there is strong evidence that they are reproductively isolated at the level of mate recognition and therefore do not produce hybrids (Morewood, submitted). We hope that the descriptions and illustrations provided here will help to prevent future misidentifications.

Natural History

Gynaephora species are among the most conspicuous insects on the high arctic tundra and observations on their natural history have been recorded ever since the early arctic expeditions of European explorers. The first comprehensive study of *G. groenlandica* was conducted by Kukal (1984) and later published by Kukal and Kevan (1987). That study provided a significant advance in knowledge of the natural history of this species; however, it did contain some gaps and inaccuracies due, in part, to the fact that it was conducted during a single summer season (see also Morewood & Ring, submitted).

Kukal and Kevan (1987) identified mortality factors and estimated mortality rates for most of the life stages of *G. groenlandica*; however, the only mortality factor they identified for eggs was "inviability." With respect to eggs, their study included only "six females observed in nature [which] remained on their cocoons and deposited all of their eggs there" and they concluded that the "eggs hatched within several days of their deposition" without presenting any relevant data (Kukal & Kevan 1987). They apparently found no other eggs masses in the field and this may be due to the facts that eggs are often laid after the female has left her cocoon, such eggs are extremely cryptic, and egg masses laid on cocoons are extremely vulnerable to predation by birds. Egg masses on cocoons are likely to be removed before they are found and, considering the rate of predation recorded in 1994, it seems likely that very few eggs laid on cocoons would escape predation long enough to hatch.

It has been known for some time that larvae of *G. groenlandica* limit their activity to the early part of the growing season (Kukal & Kevan 1987). In contrast, the fact that larvae of *G. rossii* are active late in the growing season has not been reported previously from the Arctic, although Schaeffer and

Castrovillo (1979) reported larvae of *G. rossii* to be active and feeding in September on both Mt. Katahdin, Maine, and Mt. Daisetsu, Japan. This contrast in seasonal activity may have significant consequences for the respective life cycles of the two species and there are indications that it is consistent across the Canadian Arctic. We collected *Gynaephora* larvae in the vicinity of the Muskox River on north-central Banks Island in early August of 1993 and this collection consisted of approximately two dozen larvae of *G. rossii* but only a single larva of *G. groenlandica.* In addition, researchers working on the Fosheim Peninsula of west-central Ellesmere Island in 1996 observed larvae of *G. groenlandica* in abundance in late June and early July but larvae of *G. rossii* only in early August (A. Lewkowicz, Department of Geography, University of Ottawa, pers. comm.).

Larvae of *Gynaephora* are clearly opportunistic feeders, accepting a wide variety of plant species as food, but do show definite preferences in their choice of foodplants. Curtis (1835) originally reported that larvae of *G. groenlandica* (reported as *G. rossii*) fed mostly on *Saxifraga tricuspidata* Rottböll and *S. oppositifolia,* but the preference of this species for *Salix* has since been noted repeatedly (Wolff 1964, Kukal & Kevan 1987, Kukal & Dawson 1989). The relatively few feeding observations for *G. rossii* in this study probably underestimate the variety of plants that these larvae actually eat, even at Alexandra Fiord. This widely distributed species has been reported to feed on many different plants, ranging from sedges to broad-leaf trees (Schaefer & Castrovillo 1979 and references cited therein) and it has been suggested that some isolated alpine populations show preferences for ericaceous plants, which predominate in alpine habitats (Schaefer & Castrovillo 1979).

One of the hypotheses proposed to explain why larvae of *G. groenlandica* cease feeding and become dormant so early in the growing season is that they restrict their feeding activity to the early portion of the season when the available food has the greatest nutritional value and become dormant when the benefits of continued feeding on foodplants of declining quality are outweighed by the metabolic costs of remaining active (Kukal & Dawson 1989). This hypothesis is supported by observations that larvae of *G. groenlandica* feed primarily on buds, expanding leaves, and developing catkins of *S. arctica* (Kukal & Dawson 1989; this study), a food source that rapidly declines in nutritional value as the leaves and catkins mature (Kukal & Dawson 1989, Dawson & Bliss 1993, Klein & Bay 1994). This may be considered an adaptation of this species for making the most efficient use of available food sources, given the constraints of the high arctic environment to which it is endemic. In contrast, larvae of *G. rossii* remain active late in the growing season and appear to be less particular about seeking out food sources of maximal nutritional value; however, the fact that *G. rossii* larvae consumed developing fruits, but not foliage or mature fruits, of *C. tetragona* suggests a similar selection of optimal food sources available later in the summer.

The distinct double-layered structure of the cocoons of *G. groenlandica* may again represent an adaptation to its high arctic environment, allowing

the crucial life stages of pupation and reproduction to be completed within the very short growing season. These cocoons are thought to act as "microgreenhouses" and temperatures within them have been shown to be higher than both ambient temperatures and surrounding substrate temperatures (Kevan et al. 1982, Kukal 1984). Furthermore, it has been recently reported that cocoons of *G. groenlandica* significantly enhance the rate of pupal development but that those of *G. rossii* do not (Lyon & Cartar 1996). The similar pupal development times in both species found at Alexandra Fiord might be accounted for by the difference in size of pupae of the two species at this site. Without a development-enhancing cocoon like that of *G. groenlandica*, a decrease in size of *G. rossii* in the northern portion of its range may be necessary for this species to complete pupal development quickly enough to reproduce and still leave time for the resulting eggs to hatch before winter closes in.

In a recently published study of hibernacula and winter mortality, Kukal (1995) apparently contradicts her previous assertion (Kukal, Serianni & Duman 1988, Kukal & Dawson 1989, Kukal 1990, 1991, 1993, Danks et al. 1994) that larvae of *G. groenlandica* move down close to the permafrost when they become dormant in early summer. It is noteworthy that within at least some of the cages used for that study, there were deep crevices in the tundra but the larvae chose to remain on the surface and construct their hibernacula in the vegetation and litter. The significance of this is that, although it may be argued that *G. groenlandica* larvae undergo "voluntary hypothermia" by virtue of the fact that they no longer thermoregulate by basking (cf. Kukal, Heinrich & Duman 1988), temperatures within such hibernacula track ambient temperatures fairly closely (Kukal 1995). Ground-level temperatures, both ambient and within hibernacula, often exceed 20°C and even approach 30°C during sunny weather (Morewood, unpub. data). Metabolism of poikilothermic organisms in general is directly related to temperature and this has been shown experimentally for larvae of *G. groenlandica* (Kukal & Dawson 1989). The hypothesis that larvae of *G. groenlandica* move close to the permafrost where "the larval body temperatures range between 0–5°C" (Kukal 1990) and thus reduce maintenance metabolism and conserve energy reserves during their summer dormancy (Kukal 1990, 1991, 1993, Danks et al. 1994) must be re-evaluated in the light of more recent discoveries regarding the location of, and temperature conditions in, larval hibernacula.

Finally, the urticating nature of the larval hairs of *Gynaephora* has not been reported in previously published literature but has been experienced by other fieldworkers and may be much more severe than the small itchy blisters recorded in this study. Reactions experienced by other researchers working with *Gynaephora* in the field include large blisters covering most of the hands and extensive swelling and itching of the hands (B. Lyon, Department of Biological Sciences, University of Calgary, pers. comm.). It is not known whether there is any chemical basis for these urticating properties and it may be that the irritation is a simply mechanical effect of the

barbed hairs, as has been reported for the similar, although not closely-related, larvae of *Lophocampa argentata* (Packard) (Arctiidae) (Silver 1958). As noted above, the severity of reported reactions to *Gynaephora* varies widely among different individuals and therefore researchers who plan extensive work involving exposure to the larval hairs would be well-advised to exercise caution.

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